

The University of Chicago

MORPHOLOGY OF THE SPOROPHYTE
OF RICCIA CRYSTALLINA

A DISSERTATION SUBMITTED TO THE
GRADUATE FACULTY IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

By
FRANCIS MARION PAGAN

Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS

Reprinted from
THE BOTANICAL GAZETTE
Vol. XCIII, No. 1, 1932

The University of Chicago

MORPHOLOGY OF THE SPOROPHYTE
OF RICCIA CRYSTALLINA

A DISSERTATION SUBMITTED TO THE
GRADUATE FACULTY IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

By
FRANCIS MARION PAGAN

Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS

Reprinted from
THE BOTANICAL GAZETTE
Vol. XCH, No. 1, 1932



Digitized by the Internet Archive
in 2026



MORPHOLOGY OF THE SPOROPHYTE OF *RICCIA* *CRYSTALLINA*

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 429

F. M. PAGAN

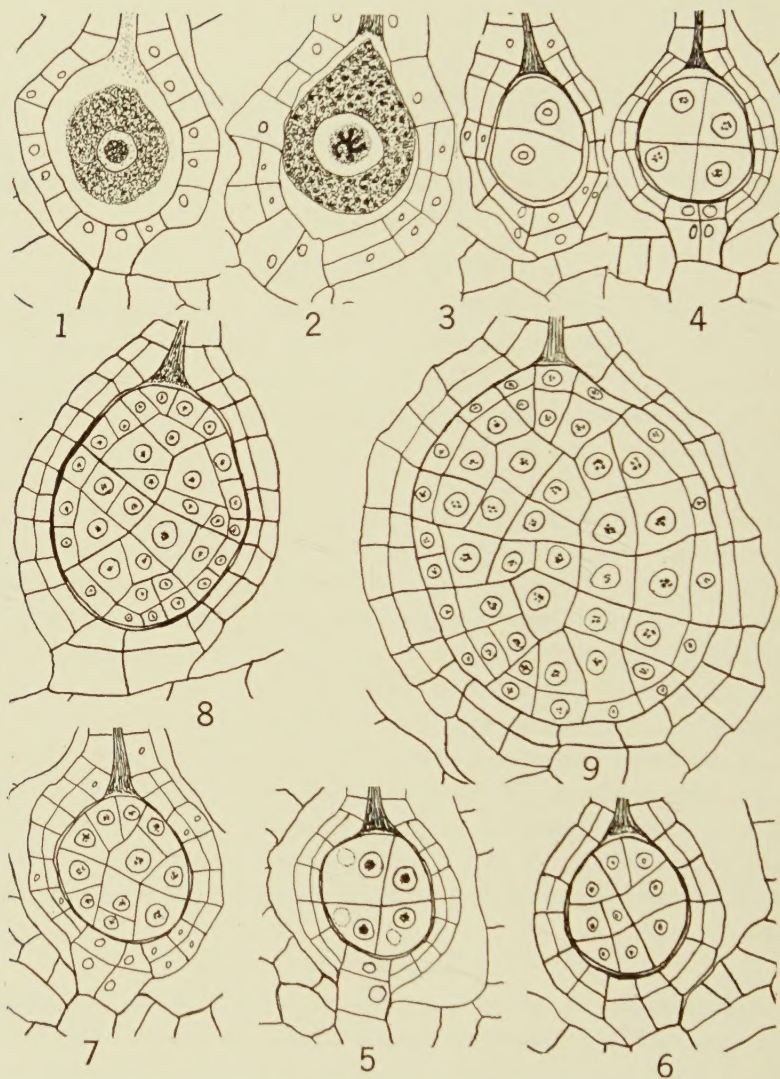
(WITH TWENTY-FOUR FIGURES)

The earliest studies of *Riccia* were probably made by HOFMEISTER (9), who studied the development of the thallus, the origin and position of the sex organs, and the development of the sporophyte. KNY (12) studied the apical cell, the method of growth of the thallus, the origin and growth of the ventral scales and sex organs, and the nature of the air cavities. LEITGEB (14) to a limited extent studied the development of the sporophyte. KIENITZ-GERLOFF (10) traced the early developmental stages of the sporangium in many members of the Hepaticae, such as *Riccia glauca*, *Marchantia polymorpha*, *Pellia epiphylla*, *Frullania dilatata*, *Preissia commutata*, and *Grimaldia bifrons*. In all cases he studied the transformation from the unicellular embryo into a mass of cells in which the various parts of the sporangium were still undifferentiated.

In more recent years a number of investigations (2, 3, 4, 5, 6, 8, 15) have been made on the morphology of several species of *Riccia*. Although the literature on various species of the genus is extensive, aside from the studies of LEITGEB (14) and LEWIS (15), no other work has been found dealing with the morphology of *Riccia crystallina*.

Fertilization

Actual union of gametes was not observed in *Riccia crystallina* but stages just before and just after fertilization were seen frequently. Fig. 1 shows a stage before fertilization, while fig. 2 represents one after fertilization has taken place. By a comparison of the mature egg (fig. 1) and the zygote (fig. 2), one can readily observe the marked changes which take place in both the zygote and venter as soon as fertilization occurs. The young embryo enlarges considerably, almost filling the cavity of the venter. A thin wall is also secreted by



FIGS. 1-9.—Fig. 1, mature egg just before fertilization; fig. 2, zygote getting ready for first division; cells of venter forming 2-layered calyptra; $\times 1230$. Fig. 3, first division of zygote; figs. 4, 5, quadrant and octant stages; fig. 6, further divisions of young embryo, fig. 7, beginning of setting off of sporangium wall; figs. 8, 9, complete differentiation of sporangium wall; $\times 775$.

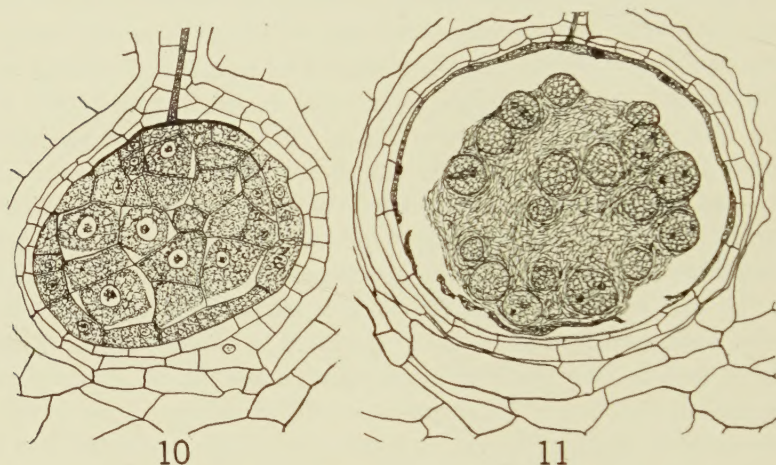
the protoplasm of the zygote. Simultaneously with these changes, the cells of the venter undergo enlargement, and soon divide by walls parallel to the surface, forming a 2-layered calyptra. These changes are so rapid that this condition may be attained even before the zygote has completed its first division.

Development of sporophyte

The first division of the zygote is either transverse or inclined to the major axis of the archegonium, thus dividing the young embryo into two almost equal cells, a hypobasal and an epibasal cell (fig. 3). The second wall that comes in is more or less perpendicular to the first, forming a quadrant (fig. 4). BLACK (3), working with *Riccia frostii*, reported this division as sometimes being parallel to the first, thus giving rise to a 3-celled embryo. In the case of *Riccio-carpus* (*Riccia*) *natans*, GARBER (6) and LEWIS (15) found that walls sometimes appeared in both the hypobasal and epibasal cells parallel to the first wall, forming a tier of four horizontally superimposed cells. Following formation of the quadrant, a wall meets the other two at right angles, resulting in the octant stage (fig. 5). From work on various members of the genus, it is evident that two types of embryos occur, the filamentous and the octant type, the latter being more common.

Further divisions of the sporophyte take place in all planes until a more or less globular mass of cells is formed (figs. 6-9). By periclinal divisions the sporangium wall, consisting of a single layer of cells, is separated from the sporogenous tissue. As a general rule, the sporangium wall is set off early (figs. 7, 8). BLACK found that it was not differentiated until late in some cases. As the sporophyte continues its growth, the sporogenous cells increase in size and divide until a rather large mass of cells is produced (fig. 9). In *Riccia crystallina*, however, the number of cells ultimately transformed into spore mother cells is much smaller than in some other members of the genus. While these potentially sporogenous cells grow and divide in all directions, those of the sporangium wall grow mainly in length and breadth, and divide only by radial divisions, so that at no time is the sporangium wall more than one cell thick (figs. 8-10). While cell multiplication and enlargement have been

going on, the cells of the thallus, calyptra, and sporangium wall have been increasing in numbers, and thus expansion of the sporogenous tissue has been possible throughout its entire development. As soon as the sporangium wall grows away from the mass of spore mother cells, these round off, increase in size, and reduction divisions occur. While these are taking place, the walls separating the spore mother cells begin to disintegrate, so that by the time the first reduction



FIGS. 10, 11.—Fig. 10, spore mother cells beginning to round out; $\times 420$. Fig. 11, spore mother cells surrounded by nutritive material and undergoing first reduction division; sporangium wall partly resorbed; $\times 295$.

division takes place the spore mother cells lie free within the cavity of the sporangium (fig. 11). These spore mother cells are surrounded by much nutritive material. This substance, which serves as food for the developing spore mother cells, may be said to come from four sources: storage products of photosynthesis within the cells of the gametophyte, disorganization of the cells of the sporangium wall and calyptra, decomposition products of the cell walls between the spore mother cells, and disintegration of some of the spore mother cells themselves.

The disintegration of the sporangium wall is varied. In *Riccia frostii*, BLACK found that by the time the spore mother cells were formed the sporangium wall (amphithecium) was partially

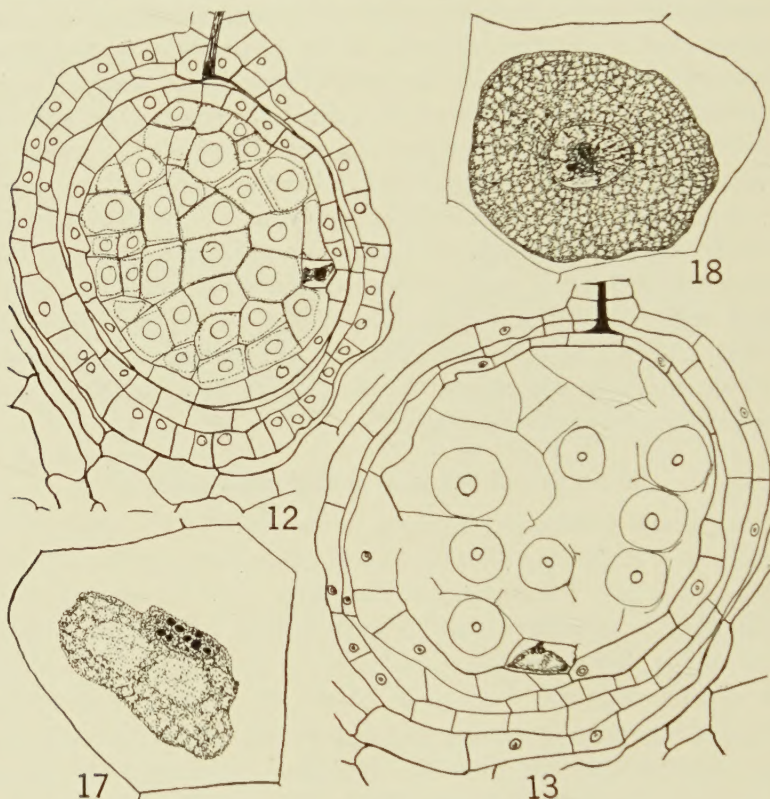
disorganized; while in *R. natans* GARBER and LEWIS found that it was distinguishable until the spores were almost ripe. In *R. crystallina* this layer in some cases begins early to disintegrate, while in others it remains intact until the spore mother cells are ready for reduction divisions. Apparently the late disappearance of the sporangium wall is coupled with the failure of potential sporogenous tissue to produce spores. It has been observed that when there is a diversion of potential sporogenous tissue the sporangium wall remains intact for a long time (figs. 13, 14). This behavior seems to indicate that the whole phenomenon of diversion of potential sporogenous tissue is a question of food supply, as will be dealt with in another part of this paper. Disintegration of the inner layer of the calyptra takes place in much the same manner as that of the sporangium wall. Finally the remaining layer of the calyptra is resorbed and the mature spores are left free in the archegonial chamber. The spores can escape only by decay of the thallus, one of the most primitive methods of spore dispersal.

Diversion of potential sporogenous tissue

One of the outstanding features connected with the sporophyte in species of *Riccia* has been the lack of sterile tissue, aside from the sporangium wall. All students of the group, up to the present time, have been in agreement that all spore mother cells in *Riccia* produce spores. For many years Professor W. J. G. LAND has been of the opinion that the beginnings of the diversion of potentially sporogenous tissue was to be found in *Riccia*. Slides of *R. crystallina* were prepared by him but through a period of many years most of these original slides were lost. The few remaining, in addition to some material already imbedded in paraffin, Professor LAND very kindly turned over to me. After a critical study of this material, enough evidence has been found to indicate that in *R. crystallina* some of the spore mother cells fail to produce spores.

The diversion of potential sporogenous tissue in *Riccia crystallina* can be observed at different periods during development of the sporophyte. Fig. 12 represents a rather early stage in which the spore mother cells are just beginning to round out. The protoplasmic content of the diverted sporogenous tissue (one cell in this case)

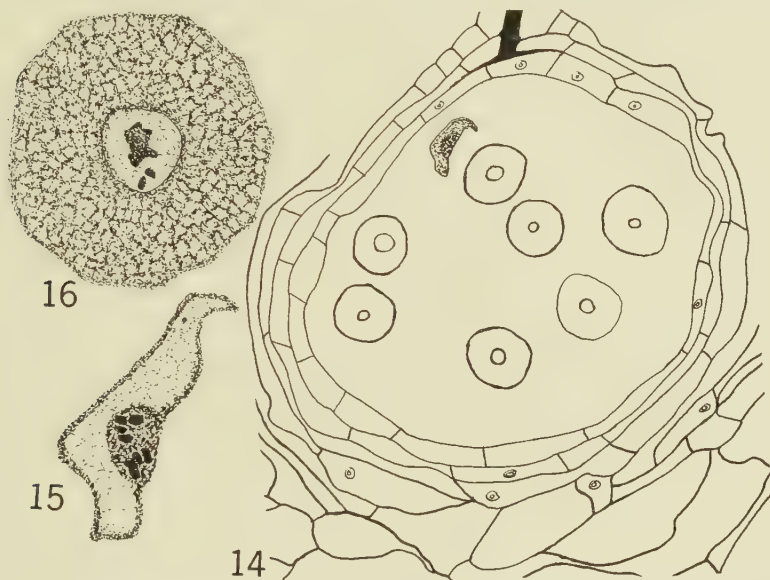
has withdrawn to the center of the cell, the nuclear material has begun to disorganize, and disintegration of the protoplasm is evident, as compared with that of its sister cells in which no disturbance has yet taken place. The staining reaction is also different,



FIGS. 12, 13, 17, 18.—Fig. 12, sporangium showing diversion of potential sporogenous tissue at early stage in spore mother cell formation; $\times 660$. Fig. 13, diversion of spore mother cell in hypobasal region of sporangium; $\times 510$. Figs. 17, 18, sterile and spore mother cells respectively, taken from same sporangium; sterile cell shows eight masses of chromatin but nuclear membrane has already disappeared; $\times 1920$.

perhaps because of the decomposition products. The sterile or nurse cells, as they may be called, stand out conspicuously. Complete disappearance of these cells is soon accomplished and no trace of them is left, a fact which may account for their having been overlooked for so many years.

Diversion of potential sporogenous tissue is not confined to this early stage, but in the majority of cases and with greater frequency takes place later, when the spore mother cells have become somewhat spherical (figs. 13, 14). Here again these cells, which serve as food for the developing spore mother cells, are still easily recognized, not only because of the deeper staining which they take owing to the decomposition products of the nuclear and cytoplasmic substances,



FIGS. 14-16.—Fig. 14, sporangium in spore mother cell stage showing sterile cell in epibasal region; $\times 510$. Fig. 15, enlarged view of sterile cell of fig. 14; fig. 16, spore mother cell of sporangium of fig. 14; $\times 1920$.

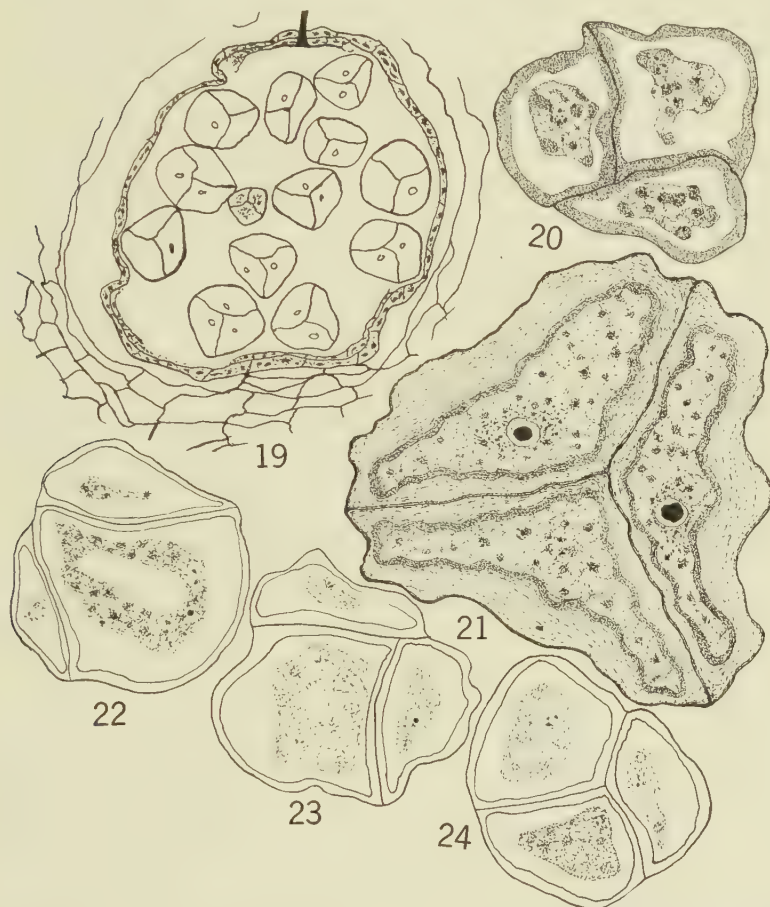
but also because of their irregular outline and smaller size compared with the mother cells as shown in figs. 15-18. Here the beginnings of sterilization have taken place much later than in the previous case. In these instances the nuclear membrane has been resorbed, but the chromatin material is still present in the form of masses, eight of which are commonly seen. These masses of chromatin doubtless represent the eight chromosomes characteristic of the sporophytic generation of this species, as reported by LEWIS and frequently observed during the present investigation. Although the figures give the impression that only one cell in a given section fails to go through

reduction division, such is not always the case. Here and there in a given section two or more sterile cells are evident, this being especially true of tangential sections. In a truly median section one sterile cell and possibly portions of one or several more are often seen.

Fig. 19 exemplifies another case in which the disturbance causing sterility appeared still later than in the two previous cases. In this instance sterilization took place rather late, when reduction division was already in progress, and consequently the spore mother cell reached the tetrad stage. However, the nucleus of each spore of the tetrad failed to organize as such, the spore coat did not attain its full development, and the tetrad as a whole remained stunted in contrast to its sister tetrads where full development was accomplished in the usual way (figs. 20, 21). These two tetrads were drawn from the same sporangium which is shown in fig. 19. Diversion of sporogenous tissue in this case approaches closely the formation of sterile cells in *Sphaerocarpus terrestris*, as reported by LECLERC DU SABLON (13), with the exception that in *Sphaerocarpus* the nucleus of each spore is well organized while in *Riccia* it is not. In the latter the nuclei are represented by small portions of chromatin material without a definite surrounding nuclear membrane. Figs. 22-24 represent a series of sections of this same sterile tetrad (fig. 20) at different levels, and show the nature of the protoplasm and cell wall as well as its size in comparison with a tetrad of the same sporangium (fig. 21) where no disturbance has occurred.

In *Oxymitra* (*Tesselina*), LEITGEB (14) figured sterile cells as occurring only on the periphery of the sporangium. He stated that they were spherical, always present in small numbers, and considerably smaller than the tetrads but larger than the cells of the sporangium wall. He observed that when the tetrads were almost ripe the sterile cells were completely devoid of starch and showed signs of death. He found sterile cells also in *Corsinia*. In this case the somewhat elongated or spindle-shaped sterile cells were distributed throughout the sporangium, and their contents consisted of fine granular protoplasm. In *Sphaerocarpus* LEITGEB showed that sterile cells were scattered through the entire sporangium, and were not, as PETOUNNIKOW (17) thought, confined to the periphery. LECLERC DU SABLON found that in *Sphaerocarpus* the sterile cells divid-

ed into four, and that such division was generally accompanied by wall formation. Whether or not this division is meiotic remains to be proved. In *Riccia crystallina* sterile or nutritive cells appear not



FIGS. 19-24.—Fig. 19, sporangium in tetrad stage showing sterile tetrad in center; $\times 295$. Figs. 20, 21, sterile and spore tetrads respectively, taken from sporangium of fig. 19; figs. 22-24, sterile tetrad of fig. 20 at different levels; $\times 1920$.

only on the periphery of the sporangium, but also rarely in the interior. It has also been observed that these nurse cells may or may not reach the tetrad stage, the latter condition being the prevalent one. The presence of sterile cells is considered of general occurrence

in *Tesselina*, *Corsinia*, and *Sphaerocarpus*, but of common rather than of general occurrence in *Riccia*. Thus the sterile cells in these species have one or more characters in common, which serve to strengthen the relationships thought to exist among these lower groups of plants. From a consideration of all the characters of the sterile cells in these groups, it may be concluded that the sterile cells of *Riccia* represent the most primitive stage of sterile cell formation so far reported, and this is in accordance with the phylogenetic position of the genus. The nutritive cells of *R. crystallina* are sister cells of the spore mother cells, as is the case in *Tesselina*, *Corsinia*, and *Sphaerocarpus*. The same condition has been reported for the elaters of *Reboulia hemisphaerica* by HAUPT (7). In all these forms the potentially sporogenous tissue is diverted much later than in *Marchantia polymorpha* and *M. domingensis*. In the former O'HANLON (16) found that the sporogenous cells which are sister cells of the elaters underwent five divisions before the spore mother cell stage was reached, while in the latter ANDERSEN (1) reported from three to four divisions. The sterile cells of *R. crystallina* represent the forerunners of the elaters of higher groups. In *Riccia* these cells are ephemeral, while in the next higher group, *Tesselina*, they remain throughout the life of the sporophyte. In the next higher group, *Corsinia*, not only are these cells permanent but they have become somewhat elongated, a condition which becomes more pronounced in the other groups. With this elongation there appear the thickenings so characteristic of the true elaters of *Marchantia*.

When the diversion of potential sporogenous tissue comes late in the life history of the sporophyte, nurse cells or elaters result; if earlier a columella is formed; if very early indeed, there is a true stele and cortex, a true conducting system. This failure of potential sporogenous tissue to produce spores is perhaps one of the most significant single facts in the phylogeny of plants, representing as it does the first step in the development of the complex conducting system of the higher plants.

It was indicated before that, when there is a diversion of potential sporogenous tissue, the sporangium wall remains intact for a longer time. Furthermore, it was assumed that this diversion was a question of food supply. Looking over the figures, it is seen that when

nutritive cells are present the sporangium wall remains until late. This behavior, therefore, seems to indicate that while sporogenous tissue is being used as food the cells of the sporangium wall have not been attacked, as is the case when no diversion of sporogenous tissue takes place. The cells of the sporangium wall serve to transport the food supplies from the calyptra and adjacent cells to the sporogenous cells for their growth. The sporogenous cells at the periphery in close proximity to those of the sporangium wall use part of this food, but the greater portion is passed on to the next cells farther away from the periphery of the sporangium. The movement of supplies is then concentric, with the cells of the sporangium wall serving as points of contact with the gametophytic tissue. This concentric movement of supplies is well shown by the sterile cells, wherein disintegration always takes place on the surface farthest away from the sporangium wall (figs. 13, 14). Thus the cells of the sporangium wall serve as conducting cells, during most of their life. Likewise some of the sporogenous cells, and especially those on the periphery, take an active part in transporting food materials from the sporangium wall to the interior; become arrested in their development; and later are used as food by their sister cells. Here then, potentially sporogenous cells are diverted to function for conduction, and ultimately their content is used by the functional sporogenous cells. In higher forms, as in the Marchantiaceae, this sterile tissue is considerably increased and is diverted to perform other kinds of work. It has given rise to new structures, namely, foot and seta, columella; and in higher forms, as *Anthoceros*, stele and cortex. There is extensive development of the foot region, it becoming larger for the purpose of procuring food. Some of the cells of the foot sometimes extend into the tissue of the gametophyte, performing the work of haustoria. The upper portion of the foot, the seta, is a transmitting region which later becomes an agent in the dispersal of spores by bursting the calyptra. In general the failure of spore mother cells seems mainly a matter of food supply, those on the periphery being deprived of their share by the neighboring cells which, while enlarging, consume great quantities of nutritive material.

It remains to account for the failure of spore mother cells in the

interior of the sporangium. Here again the question of food supply is perhaps the most important single factor. Some of the cells grow at the expense of others which, although surrounded with an abundance of nourishment, are not able to assimilate it so fast. It was observed before that, in the very early stages of the diversion of potential sporogenous tissue, the cytoplasmic contents, as well as the chromatin material, were much less in proportion to that of the cells which ultimately gave rise to spores. This condition, therefore, may be said to be, in part at least, responsible for their ultimate failure, a failure which has come rather late, when division was, if not already in progress, just starting.

Summary

1. As soon as fertilization is accomplished in *Riccia crystallina*, the young embryo enlarges considerably and a thin wall is formed. The cells of the venter also enlarge, divide, and a two-layered calyptra develops.

2. The first division of the zygote is either transverse or inclined to the major axis of the archegonium. By successive divisions, the quadrant and later the octant stages are formed. Later divisions appear in all directions, and a more or less globular mass of cells is formed. By periclinal divisions the sporangium wall is set off from the sporogenous tissue.

3. By the time the spore mother cells have attained full size, the sporangium wall, preceded by the cells of the calyptra and thallus, have grown out so that at no time has the rounding off of the spore mother cells been interfered with.

4. The spore mother cells are surrounded by an abundance of food material, all of which may be used during their period of development. This food material is derived from neighboring cells richly stored with food reserves, from the walls separating the young spore mother cells, and from spore mother cells which have failed to produce spores.

5. The resorption of the sporangium wall is varied. In some cases it begins early, but in most cases it takes place late. The time of resorption may be said to be closely connected with the food supply which is to be used by the developing spores.

6. There is a diversion of some of the potential sporogenous tissue. This diversion may take place at different times during formation of the spores. Some of the cells become abortive before they round out, others just before reduction division, and a few after division of the spore mother cells has taken place.

7. The sterile cells are not confined to the periphery of the sporangium only, but may be found in the interior as well. These nutritive cells are sister cells of the spore mother cells.

8. Diversion of potential sporogenous tissue in *Riccia crystallina* takes place much later than in *Marchantia polymorpha* and *M. domingensis*.

9. The sterile cells in *Riccia* may be considered as the forerunners of the elaters of higher forms of Hepaticae.

10. The failure of potential sporogenous tissue to produce spores seems mainly a matter of food supply.

The writer wishes to express appreciation for the advice and aid given by Professor W. J. G. LAND, who suggested this investigation and under whose direction it was carried out.

DEPARTMENT OF BIOLOGY
UNIVERSITY OF PORTO RICO
RIO PIEDRAS, PORTO RICO

[Accepted for publication July 21, 1931]

LITERATURE CITED

1. ANDERSEN, EMMA N., Morphology of sporophyte of *Marchantia domingensis*. BOT. GAZ. 88:150-166. 1929.
2. BEER, R., On the development of spores in *Riccia glauca*. Ann. Botany 20: 275-291. 1906.
3. BLACK, CAROLINE A., The morphology of *Riccia frostii* Aust. Ann. Botany 27:511-532. 1913.
4. CAMPBELL, D. H., The structure and development of mosses and ferns. 3d. ed. New York. 1918.
5. CHESEBROUGH, M. ARLOUINE, A study of a Mexican *Riccia*. BOT. GAZ. 83:99-102. 1927.
6. GARBER, J. F., The life history of *Ricciocarpus natans*. BOT. GAZ. 37:161-176. 1904.
7. HAUPT, A. W., Embryogeny and sporogenesis in *Reboulia hemisphaerica*. BOT. GAZ. 71:446-453. 1921.

8. HIRSH, PAULINE E., The development of air chambers in the Ricciaceae. Bull. Torr. Bot. Club 37:73-77. 1910.
9. HOFMEISTER, W., On the higher cryptogamia. Ray Soc. 1862.
10. KIENITZ-GERLOFF, F., Vergleichende Untersuchungen über die Entwicklungsgeschichte des Lebermoos-Sporogoniums. Bot. Zeit. 32:161-172; 193-204; 209-217; 225-235. 1874.
11. ———, Neue Beiträge zur Entwicklungsgeschichte des Lebermoos-Sporogoniums. Bot. Zeit. 33:777-782; 793-799. 1875.
12. KNY, L., Über Bau und Entwicklung der Riccien. Jahrb. Wiss. Bot. 5:364-386. 1867.
13. LECLERC DU SABLON, M., Recherches sur le développement du sporogone des hépatiques. Ann. Sci. Nat. VII. 2:126-180. 1885.
14. LEITGEB, H., Untersuchungen über die Lebermoose. Die Riccien. 4: Graz. 1879.
15. LEWIS, C. E., The embryology and development of *Riccia lutescens* and *Riccia crystallina*. BOT. GAZ. 41:109-138. 1906.
16. O'HANLON, SISTER MARY ELLEN, Germination of spores and early stages in development of gametophyte of *Marchantia polymorpha*. BOT. GAZ. 82: 215-222. 1926.
17. PETOUNNIKOW, A., Sur les organes reproducteurs du *Sphaerocarpus terrestris*. Mich. Bull. Soc. Bot. France 14:137-142. 1867.

